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AN EXPERIMENTAL STUDY ON FORAGING, MOVEMENT AND SPATIAL DISTRIBUTION IN LARVAL FISH

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ABSTRACT. Experimental data on swimming and foraging behavior of fish larvae, especially on its searching component, are summarized. The possible effects of the behavior on searching and predation rates of larvae inhabiting different types of water environment, namely the pelagic and boundary habitats, are considered. In the pelagic environment, the main mode of searching in fish larvae is a random walk that is modified by encounters of the larvae with food items and patches. Fishes use "area restricted searching" when foraging in a dense food patch, and "area increased searching" in an environment with sparsely distributed food items. In contrast to pelagic animals, boundary inhabitants, living in near-bottom or inshore waters with numerous spatially fixed objects, when foraging not only rely on current information about food distribution and composition, but also learn and map the relatively stable surroundings to improve their foraging behavior. Some results of studying the fish movement and distribution in relation to the experimental aquarium size and shape, as well as to the period after release of fish into novel surroundings are also considered.

Key words: food patches, fish larvae, pelagic habitat, boundary habitat, searching for food, area restricted searching, area increased searching, exploration of surroundings.

Introduction

Potential preys of larval fish are usually unevenly distributed. They are often clustered and form dense swarms or patches. Density of swarms is often 100 to more than 1000 times higher than the average population density (Omory and Hamner 1982). The pattern of microscale distribution of food exerts great influence on fish ingestion rate, growth and survival (Ivlev 1961, O'Connel and Raymond 1970, Hunter and Thomas 1974, Vlymen 1977).

In order to exploit clumped prey efficiently, a predator needs to successfully search for food patches, to discriminate between patches basing on their profitability and to decide how long to stay in the patch. Pecularities of behavior of larval fish moving between food patches and inside them are poorly known. It is practically impossible to observe and record the behavior and spatial microdistribution of larval fish in natural environment. So, an experimental approach is usually adopted in study of larva swimming speed and path, distance of reaction to the prey, encounter, attack and ingestion rates.

Foraging behavior in patchy environment can be roughly subdivided into two components: behavior within a patch (basically ingestion), and behavior in interpatch space (basically searching). The latter component is far less investigated than the former one.

In order to review and analyse experimental data on foraging behavior of larval fish, it would be reasonable to consider these data according to different types of environment. Pelagic and boundary environments are the most clearly discriminated types from the fish orientation point of view. Fish larvae living in pelagic habitat can orient themselves during the foraging using only current information directly related to food objects. In contrast to pelagic inhabitants, boundary inhabitants live in the environment with spatially fixed objects which can be used by fish to orient themselves. Thus, in such surroundings not only current information but also previous information or spatial memory (Olton et al.1979, von Campenhausen et al.1981) may be used during the searching for food.

Studying fish movement and spatial distribution and their role in the foraging behavior, we have to take into account that experimental surroundings always contain spatially fixed boundary objects, e.g. aquarium walls. Walls and other objects significantly influence the experimental fish swimming and distribution (Sato and

Terao 1983, Csanyi and Toth 1985, Teyke 1989, Mikheev and Pakulska 1989, Mikheev and Andreev 1992). To imitate conditions of the pelagic habitat, it is necessary to study the fish behavior in the inner part of an experimental tank, far from the walls. On the contrary, studying behavior characteristic of boundary habitat we should take into account the regularities of swimming near the aquarium walls and near other spatially fixed objects.

The main aim of this review is to summarize experimental data on larval fish foraging behaviour, mainly on its searching component, and to discuss possible effects of the behavior on searching and predation rates of fish larvae in two considerably different types of water environment. Prior to consideration of experimental data on swimming and feeding behavior of fish larvae associated with pelagic and boundary habitats, some results of studying the fish movement and distribution in relation to experimental aquarium size and shape, as well as to time after release of fish in novel surroundings will be considered.

Changes in movement and spatial distribution in relation to experimental surroundings

Larval fish foraging and swimming behavior is often studied in experiments on animals transferred from holding to observational aquarium. As a result of such procedure, the fish find itself in another aquarium which may differ from the previous one by size and shape. The acclimation period preceding the experimental trial has different duration (e.g. Ivlev 1964 — 60 min, Szekely et al. 1978 — 5 min, Wanzenbock and Schiemer 1990 — 30 min). There are some data indicating conspicious changes in behavior of fish placed in an unfamiliar environment (Welker and Welker 1958, Kleerekoper et al. 1974, Warren and Callaghan 1976, Csanyi and Toth 1985). The most intensive studies of such changes in swimming characteristics were carried out on the blind cave fish *Anoptichthys jordani* (von Campenhausen et al. 1981, Teyke 1985, 1988, 1989). Swimming behavior in an unfamiliar aquarium is characterised by swimming of the fish around boundary features with higher than normal velocity and by greater swimming activity on the whole. It was suggested that after releasing in unknown surroundings, the blind cave fishes at first explored their environment for several hours, and during this time formed a representation, or an internal map of it. Teyke (1989) has suggested that fishes in general are able to map their environment by exploring it.

In order to estimate the possible influence of aquarium size and shape on fish swimming characteristics, we studied swimming of the appropriate laboratory subject, guppy, *Poecilia reticulata* (age 1-50 days) in square aquaria (wall length: 4, 12, 24, 45, and 80 cm) and rectangular aquaria of constant volume (100 and 576 cm^2) and variable perimeter. Mean swimming speed (SS, cm s^{-1}) increased linearly with the wall size (L, cm). Regression equations are:

Fish age, days		
1	SS=0.316 + 0.022 L;	r=0.96; n=23
15	SS=0.443 + 0.029 L;	r=0.91; n=66
30	SS=0.418 + 0.037 L;	r=0.94; n=86
50	SS=0.281 + 0.046 L;	r=0.98; n=38

Swimming activity (swimming time/total time) did not depend on the aquarium size and was about 90 %. Mean swimming speed positively correlated with the perimeter of rectangular aquaria (r_S=0.64; n=32; significant at $p < 0.01$); there was no correlation between SS and the aquarium square in this case. Simple model is proposed to calculate SS in an rectangular aquarium with dimensions A × B if SS values in square aquaria A × A and B × B are known:

$$SS(AB) = A+B/T(A)+T(B),$$

where T(A)=A/SS(A) and T(B)=B/SS(B) are the periods during which the fish covers distances A and B with the speed SS(A) or SS(B), respectively.

The second aim of our preliminary experiments was to estimate the duration of period from the releasing in novel aquarium to the moment when the fish behavior became relatively stable; i.e. the duration of an acclimation period prior to registration of routine swimming behavior.

Mean swimming speed and percentage of time when fish swam along the boundary of aquarium (PT, %) gradually decreased with the increase of time following release of juvenile guppies (aged 3, 10 and 30 days) in unfamiliar surroundings. There was a highly significant ($p < 0.01$) positive correlation between SS and PT (r_S changed from 0.80 to 0.96 in different experiments). SS was related to T(time after releasing in a novel aquarium, hours) as

$$SS=a + b\ lnT$$

Coefficient "a" was equal to 0.983, 0.967, 1.016, and b — -0.160, -0.188, -0.263 for 3, 10 and 30 days old guppies, respectively.

Taking into account these results and the data

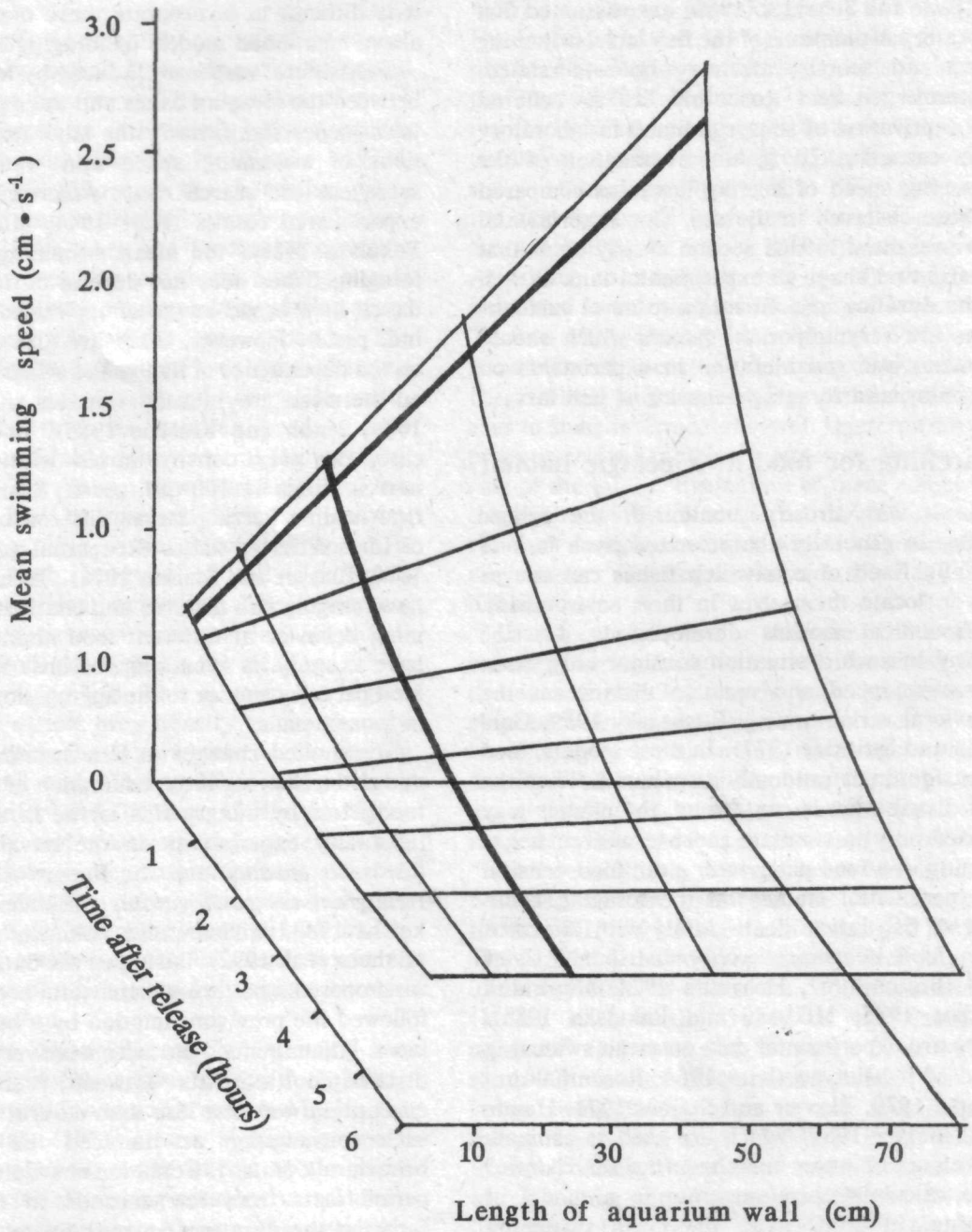

Figure 1. Swimming speed, aquarium size and the time after release in unfamiliar surroundings in guppy aged about 2 weeks. Solid lines show the data obtained experimentally.

on relationship between mean swimming speed and aquarium size, a 3-D diagram can be constructed (Fig. 1). During relatively short time after releasing in novel aquarium (not more than 1 hour), a strong dependence between swimming speed and aquarium size was observed. We hypothesize that this dependence will vanish in relatively long acclimation period (more than 3 hours).

Two phases, of high and low swimming speed, were distinguished when the time was plotted in logarithmical scale. The high activity phase lasted about 3 hours in 30 days aged guppies, 6 hours in 10 days aged and not less than 8 hours in 3 days aged guppies. Swimming activity was relatively constant or changed irregularly during the course of experiment.

According to our studies on fish swimming behavior in unfamiliar surroundings and some published data (Kleerekoper et al. 1974, von Campenhausen et al. 1981, Teyke 1985, 1988, 1989), the changes observed in swimming speed and spatial distribution can be explained by exploration and mapping of the environment. Another possible explanation may be connected with avoidance (fear) response of fish in unfamiliar surroundings (for general discussion see Russel 1973, Barnett and Cowan 1976).

Houde and Schekter (1980) have assumed that laboratory estimations of the fish larva swimming speed and search rate may be understated. Westernhagen and Rosenthal (1979) believed that deprivation of sensory stimuli in laboratory tanks caused a 20 % underestimation of the swimming speed of herring larvae as compared to those observed in the sea. Our experimental data presented in this section clearly show that the size and shape of experimental tank as well as the duration of acclimation to novel surroundings are very important factors which should be taken into consideration in experiments on swimming and foraging behavior of fish larvae.

Searching for food in a pelagic habitat

As it was already mentioned, the pelagic habitat is generally characterized by a lack of spatially fixed objects which fishes can use as cues to locate themselves in their environment. Mathematical models developed to describe feeding in such a situation consider only mean swimming speed and reaction distance as the behavioral variables (e.g. Rashevsky 1959, Gerritzen and Strickler 1977). In these models, food is considered as randomly distributed. When the food distribution is contagious, the models may be used only to simulate short-term events, e.g. foraging in a food patch with given food density.

Experimental studies on the foraging behaviour of fish larvae dealt mainly with the cases when food items are evenly distributed (Ivlev 1944, Braum 1967, Hoagman 1974, Munk and Kiorboe 1985, Mikheev and Pakulska 1988). There are experimental data on mean swimming speed of fish larvae (Ivlev 1964, Rosenthal and Hempel 1970, Blaxter and Staines 1971, Houde and Schekter 1980) which are used to estimate the volume of water searched (the search rate) or to calculate encounter rate in a model of foraging. In both cases, the mean swimming speed is considered to be constant, independent of food abundance, and not influenced by interaction with prey. However, there are experimental results indicating that the swimming speed of foraging fish depends on mean density of food items (Hunter and Thomas 1974, Munk and Kiorboe 1985); it changes when hungry fish encounter prey (Thomas 1974) or a dense food patch (Hunter and Thomas 1974, Mikheev et al. 1992). Detailed experimental studies of movement in planktivorous arctic grayling (*Thymallus arcticus*) and white crappie (*Pomoxis annularis*) fed on planktonic crustacean showed strong dependence of fish swimming characteristics on each act of predator — prey interaction (O'Brien et al. 1986, Evans and O'Brien 1988). However, it is difficult to incorporate these data into the above mentioned models of foraging behavior.

Behavioural responses induced by interactions between the foraging fishes and their preys seem to influence significantly the laboratory estimations of swimming speed and water volume searched (the search rate). According to some experimental results (Ivlev 1944, Mikheev and Pakulska 1988), the mean swimming speed of foraging fishes does not depend on food abundance in a broad range of its values (10-1000 ind. per l). However, there are also some data on the dependence of fish larvae swimming speed on the mean prey density (Hunter and Thomas 1974, Munk and Kiorboe 1985). In the latter case, the prey density varied within a more narrow range (1-100 ind. per l). Search rate of first-feeding herring larvae differed by a factor of 15 in different fishes (Rosenthal and Hempel 1970, Blaxter and Staines 1971). To understand how foraging fish behaves and controls its swimming behavior at different food abundance, we have to study its swimming response to separate food particles and/or to the aggregations of them in more detail.

We studied changes in fish swimming speed and path following the consumption of individual food items by hungry fish larvae in a series of laboratory experiments on the larval goldfish, *Carassius auratus*, and the Buenos-Aires tetra, *Hemigrammus caudovittatus* (Mikheev and Pakulska 1988, Mikheev and Pakulska 1989 a,b, Mikheev et al. 1992). Basing on the data obtained we proposed a pattern of behavioral events which followed the prey consumption by a hungry fish larva. When the food particles were very sparsely distributed (intervals between predator-prey encounters were not less than several minutes), each consumption act induced the following behavioral events: 1. Cessation of swimming (this period lasts from few seconds to dozens of seconds; the duration depends on relative prey size); 2. Slow swimming with short "steps" (distance between neighbouring turns) near (not farther than 2-3 fish body lengths) the place where the food particle were consumed (the duration is not more than one minute); 3. Fast swimming with relatively long "steps" (from few minutes to dozens of minutes). During the third period, the fish swam far from the boundary intensively visiting the central part of aquarium. We regard this behavior, which leads to an increase of search rate, as "area-increased" searching. Hamner et al. (1983) reported that *Euphausia superba* altered its feeding behavior in response to dissolved chemical cues, and located patches of algal food by "area-intensive" searching. However, quantitative data were not

provided.

The period of immobility or "handling pause" after the larva seized a prey is probably caused by handling the prey. The duration of stops positively correlates with the prey size. A similar relationship was observed by Werner (1974). The behavior following the handling pause resembles "area-restricted" searching (Tinbergen et al. 1967) when the predator thoroughly searches the area adjacent to the feeding site. If the larva encounters no prey, its swimming speed increases and the search area expands. The sequence of these behavioral events was observed in relation to both moving and immobile preys.

When the intervals between predator-prey encounters are fairly long (several minutes), all three behaviors (pause, slow swimming, and fast swimming) may be observed during an interval. In this case, the mean swimming speed is relatively high because of the significant contribution of fast swimming. The longer are the intervals between encountering prey (low density of food) the higher is the mean swimming speed of foraging fish. This relationship is probably valid at low prey density (lower than 10 ind. per l) as in the experiments on the herring larvae (Munk and Kiorboe 1985) and anchovy larvae (Hunter and Thomas 1974). At higher food density and relatively short intervals between successive prey consumptions, the fish encounters its prey during the period of slow swimming (fast swimming does not occur). In this case, if a stop is short, the mean swimming speed of foraging fish practically equals the slow swimming speed.

The most drastic change in swimming was observed when fish encountered a food patch; this sharp transition was also recorded by Hunter and Thomas (1974). Low swimming speed (approximately four times as low as the mean speed of larvae swimming outside food patches) and tortuous swimming path as well as relatively frequent long stops characterized the movement inside the food patch (Mikheev et al. 1992).

To use the mean swimming speed as a variable in behavioral models (e.g. Rashevsky 1959, Dabrowsky et al. 1988) or to estimate the water volume searched, one should take into account that swimming speed in some cases may depend on food density.

It is well known that the density of available preys in the surroundings of larvae is a crucial factor for growth and survival of fish larvae (O'Connell and Raymond 1970, Houde 1978). Lasker (1975), however, reported that the density of food organisms is extremely low in the sea as compared to the threshold food density estimated in rearing experiments. Shelbourne (1957), O'Connell and Raymond (1970), and Hunter and Thomas (1974) emphasized that the patchy distribution of food organisms is important for survival of larvae. First experimental results on the relationship between the fish predation rate and the degree of prey crowding were obtained by Ivlev (1961). The greater is the aggregation of food items (at the constant mean density) the higher is the predation rate. According to available data on feeding and growth of larval northern anchovy (Hunter and Thomas 1974, Hunter 1976, Vlymen 1977), the acquisition of energy by foraging fish grows as the crowding parameter of prey population increases to some intermediate level. Overcrowding of preys exerts an inhibitory effect on the feeding rate of the larvae. Evaluation of these somewhat controversial results requires careful consideration of foraging behavior which influences the mode of larva feeding in the case of patchy food distribution.

Let us consider firstly the role of fish larva behavior during foraging at different mean food densities. Figure 2 shows the pattern of relationship between some important features of fish larva foraging behavior and the ranges of food density. The functional response (Holling 1959) usually well fits the empirical data within the ranges of "low" and "normal" food density. At "high" density, the observed predation rate may be lower than the predicted one (Marcotte and Browman 1986, Mikheev and Pakulska 1989a). The possible behavioral mechanism inducing this inhibitory effect is either the "confusion effect" (Miller 1922, Welty 1934) or the "sensory overload" (Marcotte and Browman 1986, Milinski 1990). In very dense food patches, the fish larvae swim slowly, often turning and making frequent and long stops (Mikheev et al. 1992). In many cases, these stops are not connected with handling and consumption of prey. Within the range of "normal" food density, the mean swimming speed of a predator is moderate and relatively constant (Ivlev 1944, Mikheev and Pakulska 1988). Because of short stops and slow swimming after the consumption of prey, fish larvae swim within a relatively small area during the foraging. However, this area is larger than that in the case of dense food patch. "Area restricted" searching, which was mentioned in connection with the swimming behavior of fish larva immediately after the consumption of individual prey, is also observed for longer period in the case of "normal" and "high" food density. "Area restricted" searching in foraging fish larvae is the result of slow swimming, frequent turns and stops. Other pelagic predators can use various behavioral mechanisms to keep them-

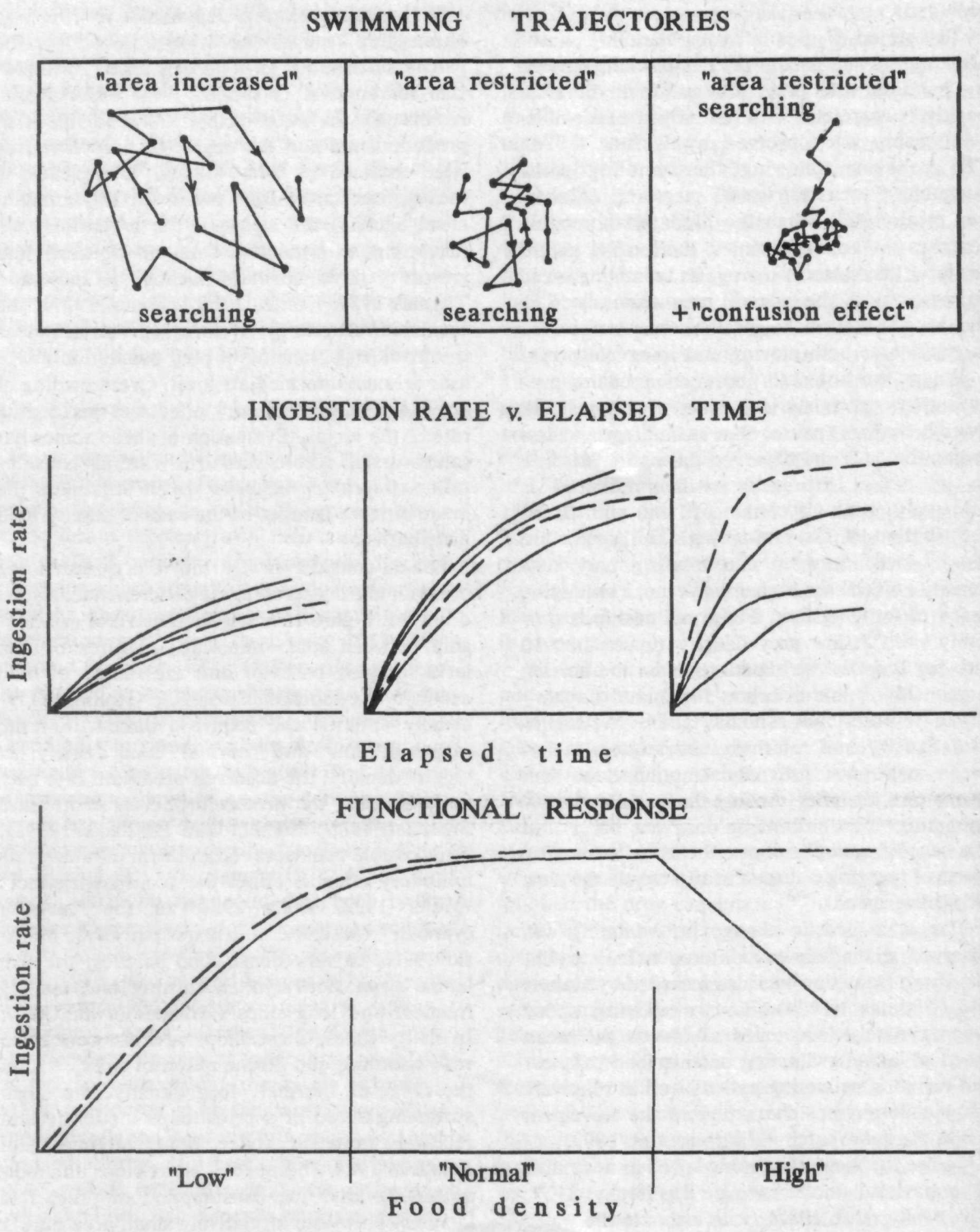

Figure 2. Foraging behaviour characteristics of fish larvae at different food density levels. Dotted lines on the middle panel show the predictions according to Rashevsky's (1959) model. Dotted line on the lower panel — Holling's (1959) type II functional response. Solid lines are based on experimental data.

selves inside the food patch. The swimming paths of copepods become increasingly turned and looped at high food concentration (Williamson 1981, Buskey 1984). The swimming speed of krill, *Thysanoessa raschii*, inside the food patch is higher than that in the lack of food (Balch et al., 1987). This fact is not trivial since a decrease in swimming speed would allow grazers to stay inside the food-rich area for a longer time. However, the krills are able to keep themselves within the algal patch by turning at the patch boundary.

"Area-increased" searching, when fish swims at higher speed (about six times over that in the

food patch) and long "steps" (about three times over that of the "area restricted" searching), occurs when the preys are sparsely distributed ("low" density). In this case (sparsely distributed food items), the search rate (estimated as the volume which fish can explore in a given period) greatly increases with the increase of both swimming speed and "step" length.

At heterogeneous food distribution, when prey organisms form patches, the larval fish behavior depends on the food patch size, food density, and the distance between patches, and/or whether individual food items are sparsely dispersed in the interpatch volume. The optimum prey distribution pattern, which maximizes the average predation rate of fish larvae, is characterized by the presence of moderately dense prey aggregations (not too dense to inhibit foraging) and sparsely distributed preys between them. Rare encounters of hungry larva with individual food items would induce "area increased" searching and promote faster finding of food patch. If the food patches are too dense and very far apart, then both excessively long searching and limited consumption would diminish the average predation rate. The discrepancy between Ivlev's (1961) and Vlymen's (1977) data presumably stems from different degrees of crowding in the respective experiments. In Ivlev's experiments, the volume of experimental tank limited the possibility of setting various food densities. Due to that, the patches were not very far from each other. However, it seems that the high patch density exerts an inhibitory effect on the consumption. In the case of most aggregated food distribution, a rise in the crowdness index from 5.8 to 9.8 causes a decrease in the relative predation rate from 100 to 98 %.

The behavioral responses of fish larvae induced by their interaction with individual preys and with aggregations of them affect the predator speed and swimming path. These responses may play a crucial role influencing the ratio between patch time and travel time, and consequently the average predation rate in the pelagic environment with patchy food distribution, where spatially fixed objects are absent.

Our results and experimental data of other authors suggest that the main searching mode of larvae foraging in pelagic environment is a random walk. It means that the larval fish swimming trajectory resembles a trajectory of Brownian particle which consists of randomly directed "steps" of variable length. Parameters of the random walk trajectory (mean swimming speed and mean length of "steps") in a fish larva are modified by swimming responses induced by encounters of hungry larva with food items and patches. Such responses are probably the main component of behavioral mechanisms controlling the search rate of fish larvae foraging in a pelagic habitat with ephemeral and uneven food distribution. Pelagic inhabitants are unable to learn and memorize surrounding features. To control the food searching process they can use only some "rules of the thumb", that is, change the swimming speed and turning rate depending on their state of satiation and the interactions with food items and patches.

Searching for food in a boundary habitat

In contrast to pelagic environment, the boundary habitats are usually characterized by the presence of spatially fixed objects which may be used by the fish as landmarks for orientation. Near-bottom or near-shore inhabitants can memorize the topology of environment by exploring it. The hypothesis of spatial memory and internal (cognitive) mapping in fish was developed on the basis of intensive experimental study of the blind fish exploratory behavior (von Campenhausen et al. 1981, Teyke 1985, 1988, 1989). Experiments supporting the hypothesis of internal map in different fish species were repeatedly reported (Wickler 1957, Welker and Welker 1958, Aronson 1971). The blind cave fish, *Anoptichthys jordani*, was shown to be able to orient itself in the spatial arrangement of experimental tank and to find the familiar feeding place even when its location is no longer directly accessible (von Campenhausen et al.1981). In a tank with two symmetrically placed gravel-filled trays, one of which containing hidden food, the goldfish, *Carassius auratus*, significantly improved the accuracy of food patch choice when some landmarks (a rock/plant combination or multicoloured plastic columns) were positioned close to the food patch or near the opposite (non-food) tray (Warburton 1990).

As to fish larvae, the experimental data on their spatial behavior and the role of it in foraging are practically absent. We studied the foraging behavior of larval goldfish, Buenos-Aires tetra, and roach, *Rutilus rutilus*, in aquaria with spatially fixed bottom food patches which consisted of immobile preys (Mikheev and Pakulska 1989b, Pakulska 1989, Mikheev and Pakulska 1991). Some experimental results obtained indicate the role of spatial behavior and spatial memory in larval fish searching for food patches.

The sinuosity of trajectory (swimming path length/beeline distance ratio) before entering the food patch decreased from the first to the

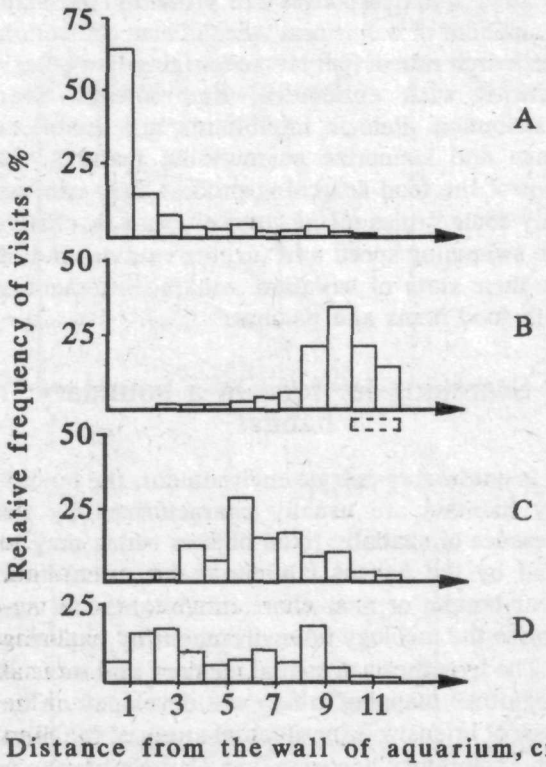

Figure 3. Frequency of visits of larval *Hemigrammus caudovittatus* to 1 cm zones of 25 x 25 cm aquarium. A — hungry fish before encountering the food patch. B — foraging in the food patch (dotted rectangular). C — 1 hour, and D — 3 hours after consumption of all the food items.

third visiting the patch (from 2.47 to 1.73, and from 2.16 to 1.61 in two experimental series with goldfish larvae fed on decapsulated cysts of *Artemia salina*). The mean swimming speed was fairly constant during all the patch searching travels (0.24 — 0.29 cm s^{-1}). Hence, subsequent fish approaches to the food patch became faster on account of the use of more advantageous (straight) swimming path rather than due to faster swimming.

Larval roach more successfully found a small patch of immobile *Artemia nauplii* during the standard experimental period (30 min) when the patch was placed near the aquarium walls (searching success was 100 % in 4 series out of 5); the searching was less successful when the patches were placed far from the walls (searching success did not exceed 86 %). The walls were conspicuous environmental landmarks which fishes could use to orient themselves in the aquarium without additional structures, especially in unfamiliar surroundings.

When hungry fish larvae found a stationary food patch they intensively fed during the first 10-20 min; subsequently the ingestion rate became slower. Searching behavior (departures and subsequent returns to the patch) was observed even in the initial period of intensive feeding. The average frequency of visiting the patch by larval goldfish was 2±1.07 (mean±S.D.) visits per 10 min during the period of most intensive feeding; in the course of foraging it increased up to 4.5±1.8 visits per 10 min. Repeatedly leaving the patch though continuing to exploit it, the larvae travelled increasingly longer distances from the patch. This behavior led to the discovery of another food patch (if there was any other patch in the aquarium).

When two food patches were found, the larvae visited both of them irrespectively of their advantage. One of the patches usually consisted of decapsulated cysts of *Artemia* while the other — of immobile nauplii of *Artemia*. Food was ad libitum in both patches. When larval goldfish consumed nauplii, the average predation rate was three times over that of consuming the cysts. While foraging inside two different patches, the fish frequently passed between them (5.3±2.5 passes per 10 min) swimming along nearly straight line. These observations indicate, firstly, the important role of current information gathering in the foraging behavior, and, secondly, the significance of previously obtained information about the environment structure in subsequent spatial orientation.

In stable environment with spatially fixed objects, the fish swimming behavior is greatly influenced both by boundary features and distribution of food patches. Larval *H. caudovittatus* consumed all preys in a small food patch in the central part of aquarium. Before the food consumption, the larva swam mainly along the walls of aquarium; during foraging and about an hour later, the predator visited the food patch and adjacent area (Fig. 3). In the absence of any food items, the fish seemed to explore the area associated with previously ingested preys by the spatial memory.

To acquire the experience, the fish larvae have to regularly explore the environment (especially the patched one) gathering information about the prey distribution and quality as well as the spatial structures (including boundary features). Thus, even if there is an excess of available food, the fish has to spend some time for sampling and consuming suboptimum preys in addition to optimum ones. This contradicts the predictions of "optimal foraging theory" (Townsend and Winfield 1985, Hart 1986) which claims that a predator has to consume only most profitable preys when they are ad libitum.

The ideal free distribution (IFD) theory (Fretwell and Lucas 1970) assumes that animals should distribute themselves between the feeding patches so that to procure food at constant rate and to maximize the energy-intake rate. In our

experiments dealt with two food patches of different quality (one being more profitable), the larvae continued visiting both of them despite the fact that the patches had been previously explored and were repeatedly visited. The fish also visited other parts of aquarium. Exploiting exclusively the most profitable patch, the larva maximizes its feeding rate but ceases to sample the environment. It is clearly that possible changes occuring in the patch as well as in less advantageous areas would be undetected and the predator would be ill-informed of alternative feeding opportunities if these areas are unvisited. To be well-informed, the predator has to continue visiting another patch in spite of the fact that it was previously assessed as less advantageous. Significant deviations from IFD predictions were reported in the case when the food patches were depleted during the course of assessment (Lester 1984) as distinct from the instances when they were not depleted (Abrahams 1989).

Unlike the pelagic animals, boundary inhabitants searching for food can use not only current information and "rules of the thumb" (i.e. searching at "area restricted" random walk movements inside food patches) but also can learn and map the relatively stable surroundings to improve their foraging and other features of behavior. Detailed analysis of the distribution and movement of larval fish during the experiment may reveal the relative contribution of previous and current experiences about the environment.

Conclusions

The analysis of foraging behavior of fish larvae in different types of environment allows to suggest that boundary inhabitants have an advantage in terms of orientation ability and food search as compared to the pelagic animals. The search and consumption rates of fish larvae in the boundary environment, where the prey distribution and composition are more predictable, may be more stable at the average. Thus, the probability of being without enough food is higher for fish larvae living in the pelagic environment with heterogeneous and ephemeral food distribution than for those living in the boundary environment containing landmarks. On the other hand, the boundary environment with numerous spatially fixed objects is also convenient for orientation of fish predators during their foraging. Hence the fish larvae inhabiting boundary biotopes appear to be more vulnerable to predation, especially inside the spatially fixed food patches. Pelagic fish larvae, in contrast to the boundary inhabitants, are more vulnerable to predators at low food density when the swimming activity of fish larvae is higher than that in dense food patches (Munk and Kiorboe 1985, Mikheev et al. 1992).

Pelagic and boundary inhabitants solve quite opposite behavioral problems connected with exploitation of food patches under the predation hazard. To minimize the threat of starvation and the vulnerability to predators, fish larvae in the pelagic environment must aim to spend more time within the food aggregations. The striking example of behavioral adaptation to patchy microalga distribution in the pelagic environment was reported by Hunter and Thomas (1974) for anchovy larvae. In dense patches of *Gymnodinium* (common food for first-feeding anchovy larvae), not only first-feeding but even yolk-sac larvae were concentrated. In a boundary habitat, the fish larvae often have to make a compromise between foraging and avoidance of predator in the vicinity of advantageous food patches. An increasing body of evidences of foraging under the predation hazard are associated with boundary habitats (Ydenberg and Dill 1986, Gilliam and Fraser 1987, Fraser and Gilliam 1987).

The above data on the behavior of fish larvae support the opinion that survival of fish larvae in the pelagic environment is influenced mainly by the food limitation. Conversely, in a boundary environment, the predation is more important limiting factor. However, the present study requires further verification, both experimental and the field.

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Экспериментальное изучение питания, движения и пространственного распределения личинок рыб

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РЕЗЮМЕ. Обобщены экспериментальные данные по закономерностям движения и пищевого поведения (в первую очередь его поисковой компоненте) личинок рыб. Проанализировано влияние поведения на скорость поиска и питания личинок, обитающих в различных биотопах (пелагические и пограничные местообитания). В пелагиали основным типом поискового поведения личинок рыб является случайный поиск, характеристики которого зависят от встреч личинки с отдельными жертвами и их скоплениями. У рыб наблюдается "локализованный поиск" при питании в плотном скоплении и "расширенный поиск" в среде с низкой плотностью жертв. В отличие от пелагических животных, обитатели пограничных биотопов, населяющие богатые ориентирами придонные или прибрежные воды, при питании используют не только текущую информацию о распределении и составе корма, но также исследуют и запоминают относительно стабильную окружающую обстановку, что может повышать эффективность поиска. Обсуждаются закономерности движения и распределения рыб в связи с экспериментальными условиями: размерами и формой аквариума, перенесением в новую обстановку.